Landscape Context Moderates Edge Effects: Nesting Success of Wood Thrushes in Central New York

MELANIE J. L. DRISCOLL*‡ AND THERESE M. DONOVAN†

*College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, U.S.A.
†Vermont Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Vermont, Burlington, VT 05405, U.S.A.

Abstract: *Despite two decades of research into the effects of habitat fragmentation and edges on nesting birds, critical information about how edges affect the success of natural nests of Neotropical migratory songbirds breeding in heterogeneous landscapes is still missing. We studied abundance and nesting success in Wood Thrushes* (Hylocichla mustelina) *breeding across a heterogeneous landscape in central New York from 1998 to 2000 to test the hypothesis that edge effects on nesting passerines are stronger in fragmented than contiguous landscapes. We monitored nests to estimate nesting success in edge and interior habitats in both fragmented and contiguously forested landscapes. In contiguous landscapes, daily survival rate did not differ between edge nests (0.963) and interior nests (0.968) ($\chi^2 = 0.19$, p = 0.66). In contrast, in fragmented landscapes, daily survival estimates were higher in interior (0.971) than edge (0.953) nests ($\chi^2 = 3.1$, p = 0.08). Our study supports the hypothesis that landscape composition moderates edge effects on actual nests of birds but does not determine the mechanisms causing these patterns.*

El Contexto del Paisaje Modera los Efectos de Borde: Éxito de Anidación de *Hylocichla mustelina* en New York Central

Resumen: *No obstante dos décadas de investigación sobre fragmentación de hábitat y efecto de borde sobre aves anidantes, aun se carece de información sobre el efecto de borde sobre el éxito de nidos naturales de aves migratorias neotropicales que se reproducen en pasajes heterogéneos. Estudiamos la abundancia y éxito de anidación de* Hylocichla mustelina *en un paisaje heterogéneo en el centro de New York de 1998 – 2000 para probar la hipótesis de que el efecto de borde sobre paserinas anidantes eran mayores en paisajes fragmentados que en continuos. Monitoreamos nidos para estimar el éxito en hábitats de borde y de interior en paisajes tanto con bosques continuos como discontinuos. En paisajes continuos, la tasa de supervivencia diaria no difirió entre nidos de borde (0.963) y nidos de interior (0.968) ($\chi^2 = 0.19$, p = 0.66). En contraste, en paisajes fragmentados, las estimaciones de supervivencia diaria fueron mayores en nidos del interior (0.971) que del borde (0.953) ($\chi^2 = 3.1$, p = 0.08). Nuestro estudio soporta la hipótesis de que la composición del paisaje modera los efectos de borde sobre nidos de aves, pero no determina los mecanismos que causan estos patrones.*

Introduction

Habitat fragmentation and edge effects are putative threats to population viability for a variety of wildlife species. Documented declines of some migratory bird species over the past three decades (Robbins et al. 1989; Askins et al. 1990; Peterjohn et al. 1995) have resulted in numerous studies of how fragmentation affects the nesting success of populations. Here, we define nesting success as the probability that a nest will fledge at least one parental offspring. For example, at a landscape scale, the nesting success of many forest bird species is significantly and positively correlated with the amount of forest cover (Donovan et al. 1995; Robinson et al. 1995; Bayne & Hobson 1997).

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Numerous studies of edge effects, defined as an increased probability of nesting failure near habitat edges, also have been conducted. However, the impact of edges on nesting success remains unclear. At a patch scale, studies of edge effects on nesting success yield conflicting results (Paton 1994; Hartley & Hunter 1998). For example, in a review of 55 studies investigating edge effects, 13 (24%) showed negative edge effects, 32 (58%) failed to detect edge effects, and 10 (18%) had mixed results (Lahti 2001).

Andrén (1995) proposed that landscape composition, the amount of different patch types in the landscape, might explain the variation in results of edge-effects studies and found that edge effects in Europe are more common in forest-farmland mosaics than in forest mosaics characterized by stands of varying ages. In North America, increases in nest predation along forest-agricultural edges are more commonly found in landscapes with low forest cover than in landscapes with high forest cover (Donovan et al. 1997; Hartley & Hunter 1998). Thus, there is an emerging pattern in investigations of habitat fragmentation that the occurrence of edge effects, especially across forest-field edges, depends on the composition of the landscape in which the edge is embedded (Lahti 2001).

Yet the generality of this pattern—that edge effects are context-dependent—is still uncertain. To our knowledge, how forest-field edges depress the success of natural nests in different landscape types is poorly understood. In most studies, edge effects have been examined through the use of artificial nests (for review, Paton 1994; Andrén 1995; Major & Kendal 1996; Lahti 2001), which facilitate experimental designs that require large sample sizes and spatial replication. However, artificial nests may be subject to different predation pressures than natural nests (Willebrand & Marcstrom 1988; Roper 1992) and may not reflect the nesting success of an actual bird species (King et al. 1999; Thompson et al. 2000). Thus, critical information about how edges affect the success of natural nests of birds in heterogeneous landscapes is still lacking.

To address these issues, we evaluated the success of 230 Wood Thrush (*Hylocichla mustelina*) nests in edge and interior habitats in both fragmented and contiguously forested landscapes in central New York. The Wood Thrush, a Nearctic Neotropical migratory songbird, is an ideal species for separating the effects of fragmentation and edge. Although Wood Thrushes may occur less frequently in small forest fragments (Temple 1986), these nest-site generalists readily settle in many landscape and forest habitat types (Weinberg & Roth 1998).

Our objectives were to (1) compare the abundance and nesting success of Wood Thrushes in fragmented and contiguous landscapes; (2) compare Wood Thrush abundance and nesting success in edge and interior habitat in each landscape type; and (3) to use actual nest data to test the hypothesis that edge effects are stronger in fragmented landscapes than in contiguous landscapes.

Methods

Study Area

We conducted our study within a five-county area (23,622 square km) in central New York in the northeastern United States (Table 1; Fig. 1). In this region, forest and agricultural lands are intermixed, such that at low levels of fragmentation, a forested matrix is interspersed with small agricultural patches, and at high levels of fragmentation, forest patches interrupt a primarily agricultural matrix. Forest patches, areas of mostly continuous forest bounded by a dissimilar habitat type (McGarigal & Marks 1995), were deciduous and mixed-deciduous stands composed primarily of maples (*Acer* spp.), ashes (*Fraxinus* spp.), and hickories (*Carya* spp.).

Study Design

We used a two-by-two factorial design to address our research questions. The two factors were landscape composition (fragmented vs. contiguous) and habitat type (edge vs. interior habitat). Landscape composition was defined as the amount of forest habitat within 5 km of a study site because a meta-analysis revealed that the relationship between daily predation rates and forest cover was most significant at this scale (Hartley & Hunter 1998). The two levels of landscape composition were generically defined as fragmented and contiguous. Fragmented sites were characterized by low forest cover, high amounts of edge, small patches, and little core area, whereas contiguous landscapes were characterized by high forest cover, low amounts of edge, large patches, and high core area (Table 2). The two levels of habitat type in the study design were interior (forest habitat > 200 m from a forest-field edge), and edge (forest habitat within 200 m of such an edge). Although study sites were selected by design to be classified as either fragmented or contiguous, the classification of edge versus interior nests was done a posteriori. We used an optimization procedure to determine the edge width that maximized the difference in nesting success between edge and interior nests.

To select study sites that met our landscape criteria, we analyzed the National Land Cover Dataset (hereafter, NLCD; Vogelmann et al. 2001) to ascertain the percent forest cover in landscapes of 5-km radius for each pixel (90 m^2) in a map of central New York (Fig. 1). We considered all forest types in this analysis—deciduous, mixed, evergreen, and woody wetland—because our intent was to identify landscapes that were fragmented or contiguous. While some forest types, such as conifer plantations, might not represent high-quality breeding habitat for Wood Thrushes, forest-forest edges are unlikely to expose nesting birds to hostile "matrix effects" similar to those experienced near forest-field edges.

Table 1. Site description, location, sampling years, and presence of Wood Thrushes on 16 sites studied in central New York in fragmented and contiguous landscapes, 1998–2000.

Site name (abbreviation)	Type of property	Landscape composition	Forest cover in a 5-km landscape (%)	Latitude/longitude	Sample years	Wood Thrush detections edge	Wood Thrush detections interior
Beaver Lake Nature Center (BL)	nature center	fragmented	50	N43° 11' W76° 24'	1998–1999	x	x
Bear Swamp State Forest (BS)	state forest	contiguous	70	N42° 45' W76° 19'	1999–2000	x	x
Baltimore Woods (BW)	nature center	fragmented	43	N42° 58' W76° 21'	1999–2000	x	x
Camillus Unique Area (CA)	unique area	fragmented	44	N43°05' W76°18'	1998–2000	x	x
Cotton Hanlon (CH)	forest products company	contiguous	77	N43° 21' W76° 32'	1999	x	x
Clark Reservation State Park (CR)	state park	fragmented	43	N42° 59' W76° 06'	1999	x	x
Cicero Swamp (CS)	swamp	fragmented	48	N43° 10' W76° 03'	1999	x	x
Cuyler Hill State Forest (CU)	state forest	contiguous	83	N42° 42' W75° 55'	1999	x	x
Green Lakes State Park (GL)	state park	fragmented	47	N43° 03' W75° 58'	1999–2000	x	x
Highland Forest (HF)	county park	contiguous	67	N42° 49' W75° 55'	1998–2000	x	
Howland Island Wildlife Management Area (HI)	wildlife management area	fragmented	49	N43° 05' W76° 41'	1999	x	x
Happy Valley Wildlife Management Area (MV)	wildlife management area	contiguous	91	N43° 27' W75° 59'	1998–2000	x	x
Labrador Hollow Unique Area (LM)	unique area	contiguous	83	N42° 47' W76° 04'	1998–1999	x	
Stoney Pond State Forest (SP)	state forest	contiguous	71	N42° 54' W75° 42'	1998–1999	x	x
Tioughnioga Wildlife Management Area (TI)	wildlife management area	contiguous	67	N42° 51' W75° 50'	1998–1999	x	x
Whiskey Hollow (WH)	county sanctuary	fragmented	38	N43° 07' W76° 24'	1999	x	x

We then limited the pool of potential sites to deciduous or mixed-forest habitats, as these were thought to be primary habitats for Wood Thrush breeding (Roth et al. 1996). Because we were interested in the effects of landscape pattern on nesting success, we additionally limited potential study sites to include only those that were visually similar in local-scale habitat features in order to eliminate local-scale vegetation as a confounding factor. All study sites were separated by a minimum of 10 km to ensure no overlap in their landscapes.

Because of logistical constraints, no additional sites could be located that were within driving distance and that met our criteria for spatial separation between sites and for level of fragmentation. Thus, 16 sites were the maximum number that we had available for the study, 8 in each landscape type (Table 1).

To verify that local-scale vegetation did not differ significantly across habitat or landscape types, we measured basal area, stem density, percent ground cover, and percent canopy cover at random points across all study sites. We randomly selected 115 points in each of the fragmented and contiguous landscapes and compared each of these measures of vegetation with *t* tests (PROC TTEST, SAS Institute 1989).

Within each study site, birds were surveyed in one edge and one interior location. We called the 100-m-radius circle surrounding each survey point a study plot, and searched for all nests within plots as well as in surrounding areas. Thus, there were 32 study plots in total: each of 16 study sites contained an interior plot and an edge plot. Because of this pairing, we used split-plot analysis of variance (ANOVA) for the data analysis. The 16 plots within each landscape type were replicates for the landscape-composition factor. The 16 plots within each habitat type were replicates for the habitat-type factor.

Abundance and Nest Searching and Monitoring

We conducted 6-minute standardized point-count surveys (Ralph et al. 1993) from dawn until 1000 hours to sample Wood Thrushes within each study plot four times throughout the breeding season. Wood Thrush detections were grouped into two distance classes, <50 m and unlimited distance from the observer. Unfortunately, we could not adjust the raw counts by their corresponding detection probabilities, so counts may have been biased on the low side if not all birds were detected. However, all counts were conducted in the morning hours, in good weather conditions, and by experienced observers, and were repeated four times across the breeding season to limit this potential bias. Abundance was the maximum number of Wood Thrushes detected within the 50-m fixed radius at a study plot across the four point-count surveys.

We located and monitored nests on 16 study sites in 1999, on a subset of 7 study sites in 1998, and on a different subset of 6 study sites in 2000. To examine the
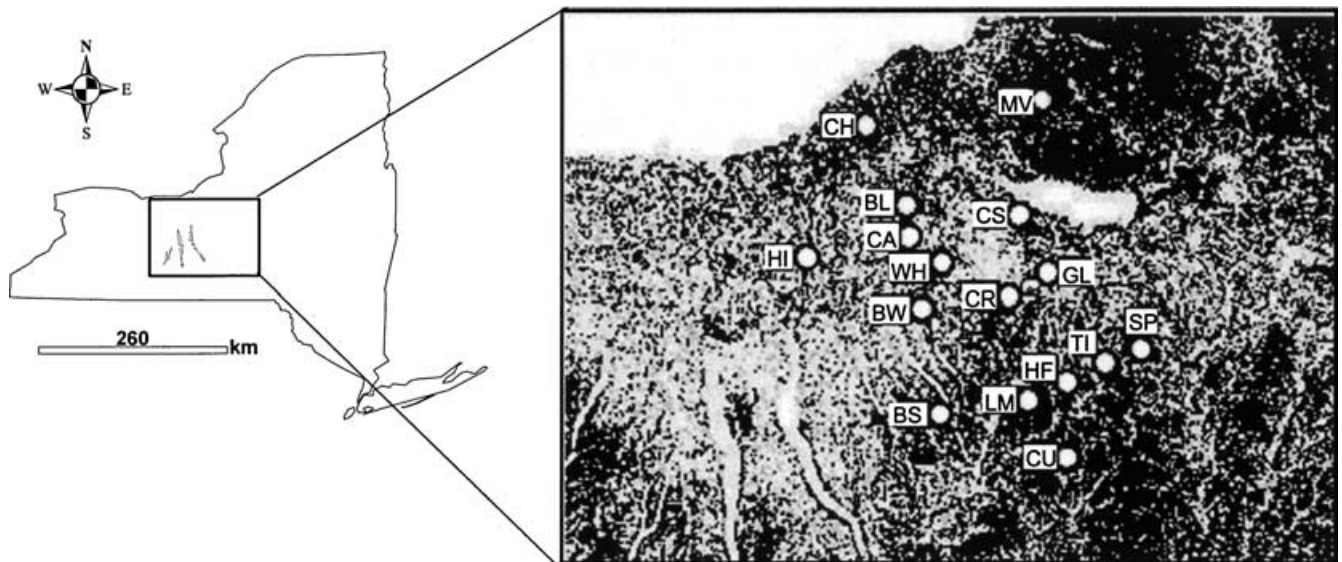
Figure 1. Map of New York with study area in box (left). Land-cover map of the study area (right) shows forested proportion of landscape in central New York, taken from National Land Cover Dataset (NLCD) produced by Environmental Protection Agency/Multi-Resolution Land Cover (EPA/MRLC). Forest pixels are gray; non-forest pixels are white. Forest consists of deciduous, mixed, evergreen, and woody wetland. All other land-cover types are considered to fragment forest cover. Locations of 16 study sites in gray circles (abbreviations for study site names in Table 1).

possible effects of density dependence on nesting success, in 2000 we intensively searched two 6.25-ha study plots in each study site in order to obtain density estimates of nests in each landscape type. We searched for nests from the first week in May until 31 July each year. Nest-initiation dates ranged from 11 May to 22 July. We located nests through systematic area searches, bird vocalizations, and behavioral cues (Martin & Geupel 1993). Each nest was monitored every 3–4 days until nest fate was ascertained. Detailed descriptions of nest contents were recorded at each nest check. A nest was considered successful if at least one host nestling fledged. Nest fate was uncertain if fledglings were not detected within 150 m

of the nest on the visit following the predicted fledge date, and if there were no indications of adults feeding fledglings within that radius. In such cases we considered a nest successful if nestlings were at least 10 days of age at the midpoint between the last two nest checks and if there was no strong evidence of nest predation (e.g., feathers or blood in the nest, nest lining pulled up from the bottom; Trine 1998).

Daily Survival Estimates and Nest-Period Success Rates

We used the Mayfield method to estimate daily survival rates of nests (Mayfield 1961, 1975). We estimated nest-period

Table 2. Results of *t* tests comparing forest fragmentation metrics in 5-km landscapes for 16 study sites in central New York, 1998–2000.

Forest Metric	Landscape	Mean (SD)	t	p
Percentage of landscape	contiguous	76.03 (8.98)	8.84	<0.0001
	fragmented	45.28 (4.03)		
Number of patches	contiguous	227.63 (118.28)	5.41	0.0003
	fragmented	795.63 (272.30)		
Total forest-field edge (m)	contiguous	423780 (142671)	5.63	<0.0001
	fragmented	772309 (101548)		
Largest patch index	contiguous	72.74 (12.03)	8.19	<0.0001
	fragmented	31.36 (7.70)		
Area-weighted mean area	contiguous	5490.20 (1165.70)	7.89	<0.0001
	fragmented	1824.40 (605.45)		
Area-weighted SD	contiguous	466.07 (292.52)	3.60	0.0085
	fragmented	92.53 (24.81)		
Total core area	contiguous	2187.60 (845.48)	6.24	0.0003
	fragmented	266.87 (206.20)		

Table 3. Results of *t* tests on the differences in measures of vegetation structure across fragmented and contiguous landscapes in central New York, 1998–2000.

Vegetation metric	Landscape	Sample size	Mean (SD)	t	p
Basal area	contiguous	115	30.85 (10.33)	1.20	0.249
	fragmented	115	25.32 (7.88)		
Percent	contiguous	115	20.75 (7.29)	1.59	0.134
ground cover	fragmented	115	28.01 (10.67)		
Stem density (no./ha)	contiguous	115	11632 (3948.30)	0.71	0.490
	fragmented	115	12889 (3097.90)		
Percent	contiguous	115	83.99 (6.74)	0.35	0.735
canopy cover	fragmented	115	82.86 (6.38)		

survival for a 28-day nest period (Roth et al. 1996). This is a conservative estimate because it includes the laying period and assumes a mean clutch size of four; it assures that our estimate of nest-period survival would not be artificially inflated.

Average Number of Young Fledged

Nests in different landscapes and habitat types may have identical probabilities of daily survival but still produce substantially different numbers of fledglings. To account for this difference, we compared the mean number of young fledged per successful nest to detect differences in initial clutch sizes or partial brood reduction. We also compared the average number of young fledged per nest (successful or failed) and used only nests located before the start of incubation to reduce the bias associated with undetected nesting failures (Mayfield 1975).

Nest Density

Nest predation may be higher in fragmented landscapes and, because of renesting, the total number of nests located through the season may be a misleading indicator of the density of breeding pairs. Therefore, we calculated nest density as the maximum number of nests active at any time during the breeding season on each of the 6.25-ha study plots in 2000.

Statistical Analysis

Because sample sizes were small, we tested for significance at the alpha level of 0.10 for all analyses to minimize the risk of overlooking a biologically significant difference. We tested for normality of abundance data using a Shapiro-Wilk test (Sokal & Rohlf 1995). We compared differences in Wood Thrush maximum abundance across landscapes and habitat types and tested for interactions using a split-plot ANOVA on average maximum detections of Wood Thrushes (PROC GLM, SAS Institute 1989).

We used the program CONTRAST to analyze differences in daily survival estimates (Hines & Sauer 1989). We tested for differences in measures of daily survival between years, and, finding none, pooled data (PROC GLM, SAS Institute 1989; CONTRAST, Hines & Sauer 1989). The

lack of difference between years may be a result of low power, but pooling the data results in temporal pseudo-replication. Because of this, we present results for each year separately as well as combined across years. Comparisons of nesting success among the habitat-landscape combinations were two fold. First, in a test similar to the overall ANOVA design, we compared the daily survival estimates for edge and interior habitat in fragmented and contiguous landscapes (four daily survival estimates). Next we conducted a priori tests of two hypotheses: that survival rates differ between edge and interior nests in contiguous landscapes and that survival rates differ between edge and interior nests in fragmented landscapes.

We used a split-plot ANOVA to compare the average number of Wood Thrush fledglings produced per nest and the average number of fledglings produced per successful nest for all combinations of landscape and habitat type (PROC GLM, SAS 1989). We used a *t* test to compare nest density in fragmented versus contiguous landscapes for 2000 only (PROC TTEST, SAS Institute 1989).

Results

Local-Scale Habitat Assessment

Though the sites differed with respect to landscape metrics (Table 2), basal area, percent ground cover, stem density, and percent canopy cover were comparable across landscape types (Table 3).

Wood Thrush Abundance and Nesting Success

The average maximum abundance of Wood Thrushes ranged from 1.25 (SD = 1.28) individuals per point count in contiguous-edge study plots to 1.63 (SD = 1.69) individuals per point count in fragmented-interior study plots (Table 4). Abundance data were normally distributed (Shapiro-Wilk test, $W = 0.97$, $p = 0.85$; Sokal & Rohlf 1995). Mean maximum abundance did not differ based on landscape (PROC GLM, $F = 0.13$, $p = 0.72$) or habitat type (PROC GLM, $F = 0.16$, $p = 0.69$; Table 4). Therefore, Wood Thrushes do not appear to be selecting territories based on these factors.

Table 4. Average maximum detections per 6-minute counts of Wood Thrushes and measures of nest success (SD) for Wood Thrushes in edge and interior habitat in high fragmentation and low fragmentation landscapes in central New York, 1998–2000.

ANOVA factor	Plot type	Number of study plots[a]	Average maximum abundance (SD) (<50 m)[b]	Daily survival (SD) (nest period)[c]	Number of nests[d]	Average young fledged per nest[e]	Number of nests[f]	Average young fledged per successful nest[g]	Number of nests[b]
Landscape composition	fragmented	8	1.56 (1.36)	0.956 (0.005) (29)	135	0.93 (1.44)	59	2.75 (0.88)	56
	contiguous	8	1.38 (1.31)	0.967 (0.005) (39)	95	1.64 (1.60)	33	3.04 (0.64)	49
Habitat type	edge	16	1.38 (1.15)	0.955 (0.005) (27)	135	0.91 (1.47)	56	2.84 (0.86)	55
	interior	16	1.56 (1.50)	0.969 (0.005) (41)	95	1.61 (1.53)	36	2.94 (0.71)	50
Interactions	fragmented edge	8	1.50 (1.07)	0.953 (0.006) (26)	110	0.84 (1.43)	50	2.79 (0.91)	43
	fragmented interior	8	1.63 (1.69)	0.971 (0.009) (44)	25	1.44 (1.42)	9	2.62 (0.77)	13
	contiguous edge	8	1.25 (1.28)	0.963 (0.010) (35)	25	1.50 (1.76)	6	3.00 (0.60)	12
	contiguous interior	8	1.50 (1.41)	0.968 (0.005) (40)	70	1.67 (1.59)	27	3.05 (0.66)	37

[a] *Number of study plots in each landscape or habitat type or each landscape-habitat type combination.*
[b] *Maximum detections of Wood Thrushes within 50 m of the observer.*
[c] *Daily survival calculated as 1-(total number of nests failed/total number of observation days) pooled across all nests within the study plot type. Nest period survival was calculated as daily survival raised to the 28th power (the length of the Wood Thrush nesting period).*
[d] *Total nest sample size.*
[e] *Mean number of fledglings per nesting attempt.*
[f] *Sample size of nests located prior to the start of incubation used to calculate average young fledged per nest.*
[g] *Mean number of fledglings per successful nesting attempt.*
[b] *Sample size of successful nests used to calculate average young fledged per successful nest.*

We found 230 nests: 105 nests succeeded and the remaining 125 failed, primarily as a result of predation (75%). Parasitism by Brown-headed Cowbirds (*Molothrus ater*) was negligible, with only 10% of nests parasitized, most receiving only one cowbird egg. We found 135 nests in fragmented landscapes (59%), and 110 (81%) of these were located along edges, despite equal search effort across landscape-habitat combinations. Ninety-five nests were located in interior habitat (41%) (Table 4).

Daily survival rate ranged from 0.953 (SD = 0.006) in fragmented-edge habitat to 0.971 (SD = 0.009) in fragmented-interior habitat ($\chi^2 = 5.15$, $p = 0.16$; Table 4 and Fig. 2). These rates translate to 26% and 44% nest period success, respectively. In contiguous landscapes, daily survival rate did not differ between edge nests (0.963, SD = 0.01) and interior nests (0.968, SD = 0.005; $\chi^2 = 0.19$, $p = 0.66$; Fig. 2). In contrast, daily survival estimates were higher among interior nests (0.971, SD = 0.009) than among edge nests (0.953, SD = 0.006) within fragmented landscapes ($\chi^2 = 3.1$, $p = 0.08$; Fig. 2). These patterns were generally consistent, although statistically not significant, when the data were analyzed by year. These results support the hypothesis that forest-field edge effects may be stronger in fragmented landscapes (Donovan et al. 1997; Hartley & Hunter 1998). Nest density was higher in fragmented landscapes (0.91 nests/ha) than in contiguous landscapes (0.40 nests/ha) ($t = 2.53$, df = 10, $p = 0.03$).

There were no significant landscape or edge effects on either the average number of young fledged per nest or the average number of young fledged per successful nest (Table 4). The number of female young fledged per successful nest was 1.31 in fragmented-interior habitat, 1.395 in fragmented-edge habitat, 1.50 in contiguous-edge habitat, and 1.53 in contiguous-interior habitat. These differences, though statistically nonsignificant, could have biological significance in terms of population viability.

Discussion

Consequences of Landscape Composition for Edge Effects

This study of Wood Thrushes is apparently the first to use natural nests of birds to examine how landscape composition may simultaneously moderate edge effects on the abundance and nesting success of birds. Wood Thrush abundance was not affected by landscape composition or proximity to edge. However, landscape composition affected the strength of edge effects on daily survival estimates for Wood Thrushes, with edge effects being stronger in more fragmented landscapes. This result was consistent but not significantly different in year-by-year analyses, but it was significant when data were pooled across years.
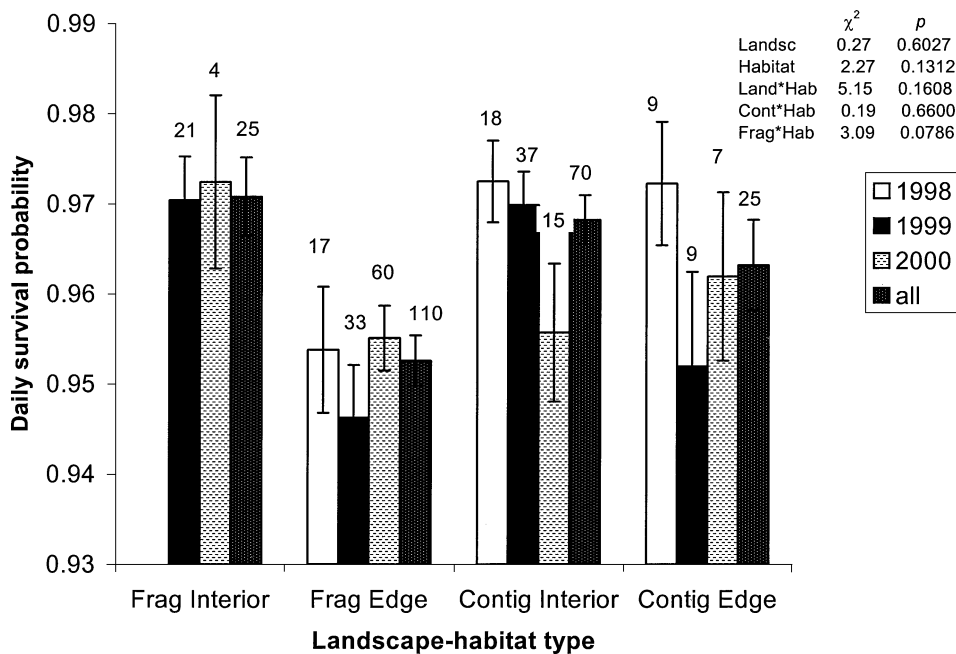
Figure 2. Daily survival probabilities for nests in each combination of landscape and habitat type, both by year and combined across all years, from central New York, 1998–2000. Sample sizes are above standard error bars. Text box shows results of chi-square tests and associated probabilities for each landscape type, habitat type, landscape-habitat combination, and habitat type within fragmented landscapes for all years combined.

Nest predation should increase with increasing predator abundance because many predators locate nests by chance (Angelstam 1986). Higher predator abundance and density (Andrén 1992; Marini et al. 1995), increased activity (Bider 1968), and an increase in generalist species (Angelstam 1986) along edges may account for higher nest-predation rates along forest edges than in forest interiors (Soderstrom et al. 1998).

If predators are more abundant along all edges, why is nest predation greater in edges in fragmented landscapes than in contiguously forested landscapes? Ecological processes such as nest predation may be influenced more by edge amount, arrangement, or density (Saunders et al. 1991) than by the mere presence of edge. For example, forest corners have more agricultural habitat in close proximity to them than straight edges (Malcolm 1994). Fragmented landscapes tend to have smaller patches; thus, a greater proportion of fragmented edge is corner-type habitat and is more exposed to hostile effects from the neighboring matrix than edge in contiguous landscapes. Therefore, fragmented landscapes, with a higher abundance of predators, may be subject to stronger edge effects or edge effects that extend farther into patches than is the case for contiguous landscapes (Andrén 1992).

Alternatively, higher rates of predation along edges in fragmented landscapes may be the result of density-dependent nest predation. Because we conducted area searches and attempted to locate all nests in a study plot in 2000, we were able to compute the maximum number of Wood Thrush nests that were simultaneously active as a measure of nest density. Wood Thrush nest density in our study was higher in fragmented landscapes than contiguous landscapes, and nests seemed to be concentrated along edges (M.J.L.D., personal observation).

Although we did not directly test this hypothesis, it is possible that density-dependent predation is a mechanism that contributes to low nesting success in fragments. Density-dependent predation is one of several alternative hypotheses that needs additional study.

Wood Thrush Distribution and Ecological Traps

Because Wood Thrushes require a fully developed understory for nesting (James et al. 1984), they may be attracted to edges and forest fragments for nesting because of vegetation characteristics therein, but they may experience reduced reproductive success in these habitats. In our study, Wood Thrushes used these lower-quality habitats for nesting. Although our point-count data did not show statistically different patterns in distribution, nest density appeared to be higher in edge habitats than interior habitats, particularly in fragmented landscapes (M.J.L.D., personal observation). Nest predation may not be the only factor limiting habitat quality on edge-dominated fragments. Burke and Nol (1998) found that insect biomass was reduced in small forest fragments, and Zanette et al. (2000) linked reduced insect biomass in small fragments with reduced foraging efficiency, egg weight, and nestling size in Eastern Yellow Robins (*Eopsaltria australis*). Therefore, while edges or fragments may be attractive nesting habitat, changes in habitat quality due to fragmentation may reduce avian fitness in the habitats, a process including increased edge-related nest predation.

Wood Thrushes in central New York may be caught in an ecological trap, perceiving fragmented and edge habitat as high in quality because structural cues are appropriate, even though anthropogenic habitat change has made the habitat unsuitable (Gates & Gysel 1978). Wood

Thrushes caught in an ecological trap would select poor-quality habitat out of proportion to its availability in the landscape. If edges, especially in fragmented landscapes, comprise a significant proportion of the available habitat in a region, this maladaptive habitat selection could lead to regional population declines. Breeding Bird Survey data show a 2% decline per year in Wood Thrushes across New York State, southern New England, and the eastern United States over the past 20 years (Sauer et al. 2003). Though nonbreeding events are known to affect survival or fitness surrogates of survival (Rappole 1995), our research suggests that selection of fragments and edges for breeding could also contribute to these declines.

Factors affecting Wood Thrushes may also affect other forest-interior breeding passerines; management for one species may benefit a suite of species with similar evolutionary pasts and life histories. Our results suggest that it is important both to conserve interior habitat in contiguous landscapes, where predation is relatively low, and to enhance the vegetation structure to increase densities of Wood Thrushes in those habitats. Additionally, it is unlikely that only the proportion of a cover type in the landscape is correlated with nesting success. Degree of fragmentation (arrangement and size of patches) within similarly forested landscapes may affect nesting success. Studies are needed to explore how different landscape factors, such as mean patch size and edge-to-interior ratio, may be managed to mitigate some of the negative impacts of fragmentation, and to explore the mechanisms that lead to differential predation rates across a landscape (Chalfoun et al. 2002).

Caveats to Nest-Success Estimates and Future Directions

Nesting success, defined as the probability that a nest will successfully fledge offspring, may be a poor estimator of birth rate—the number of offspring produced per adult per year (Thompson et al. 2001). Adult females often renest multiple times in the event of nesting failure, so low nesting success rates may or may not reflect low birth rates. Additionally, even if edge effects depress levels of reproduction, the impact of edges on a population's ability to persist across a landscape depends on the distribution of individuals across edge and interior habitat, differences in reproductive success in edge and interior habitat, and the actual amount of edge versus interior habitat in the landscape (Donovan & Thompson 2001). Therefore, the degree to which edge effects influence population viability remains an area of rich research potential.

Acknowledgments

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